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The historical demise of *Pinus nigra* forests in the Northern Iberian Plateau (south-western Europe)

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Running headline: Fire, land-use and *Pinus nigra* demise

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Summary

1. *Pinus nigra* Arn. forests dominated over extensive areas of the Northern Iberian Plateau (Spain) during the Holocene, but a strong decline during the historical period (*c.* 1300-700 cal. BP) led to the present fragmented populations. This demise has been generally attributed to land-use changes or climate, but the specific roles of disturbance regimes such as fire variability and grazing on the long-term are not fully understood yet.

2. We combine multi-proxy palaeoecological data (fossil pollen, spores, conifer stomata, microscopic and macroscopic charcoal) together with quantitative analyses (ordination and peak detection) from a high-resolution sedimentary sequence (Tubilla del Lago, 900 m a.s.l.) to assess the causes of pine forests demise. A new microscopic charcoal record from an additional sequence (Espinosa de Cerrato, 885 m a.s.l.) is used to assess burning and pine decline at a more regional (100 km radius) scale.

3. *Pinus nigra* forests could cope with drought and fire regime variability (FRI = 110-500 years), with forest recovery taking *c.* 100-200 years after fires. Only at 1300-1200 cal. BP a long-lasting irrecoverable demise of *P. nigra* forests occurred when human-induced fires together with arable and pastoral farming became widespread in the area. Subsequently, *Quercus* woodlands expanded in the remnant patchy pinewoods. This

vegetation shift was primarily caused by three particularly important fire episodes in less than a century (*c.* 1300-1200 cal. BP).

4. *Synthesis*. *Pinus nigra* forests have shown a millennial resilience to the natural fire regime of the Northern Iberian Plateau, that was characterized by relatively frequent small-moderate fires and rare high-intensity fires. However, frequent human-caused crown fires and the onset of intensive farming caused their demise over an extensive area. Ongoing land-use abandonment in the Iberian mountains could promote the occurrence of high-intensity, severe fires due to the rapid build-up of high fuel loads. Forest management could mimic the natural fire regime by periodically reducing fuel loads for a transitional period until natural disturbance variability is fully restored, thus preserving these relict native plant communities.

Key-words: charcoal, climate change, conservation ecology, fire ecology, forest management, grazing, Mediterranean, palaeoecology and land-use history, pollen, Spain

Introduction

At present, almost no trace of natural ecosystems is left in Mediterranean Europe after millennia of human-induced landscape transformation (e.g. Tinner *et al.* 1999; Colombaroli *et al.* 2008; Carrión *et al.* 2010), leaving few remnants of the original forest (Tinner *et al.* 2009; Carrión *et al.* 2010). In certain areas, keystone species of the 'pristine' Mediterranean ecosystems (such as *Abies alba* Mill., *Quercus ilex* L. or *Pinus sylvestris* L.) declined or even disappeared following land-use intensification since prehistoric times (Colombaroli *et al.* 2007; Tinner *et al.* 2009, 2013; Rubiales *et al.* 2012, 2015; Henne *et al.* 2015).

The Northern Iberian Plateau is currently one of the most deforested areas of Mediterranean Europe, with a landscape largely dominated by cereal fields, vineyards and pasturelands. Forest vegetation is restricted to scattered and usually disturbed *Q. ilex* subsp. *ballota* (Desf.) Samp., *Quercus faginea* Lam., *Juniperus thurifera* L. and *Quercus pyrenaica* Willd. woodlands. Those species are all adapted to the continental Mediterranean climate of inland Iberia (Costa *et al.* 2005). However, long-term palaeoecological data (covering multi-decadal to millennial ecosystem variability) suggest that pine-dominated forests were widespread over a wide range of soil and climate conditions during the Holocene (Franco-Múgica *et al.* 2001, 2005; García-Amorena *et al.* 2011; García-Antón *et al.* 2011; Morales-Molino *et al.* 2012; Fig. 1). Their demise mostly occurred during the medieval period (Franco-Múgica *et al.* 2001) and led to present small and isolated populations, which are often threatened and at risk of extinction (Fig. 1). Considering the long history of human occupation in the area, it is still debated which factors besides land-use led to pine forest decline by 1300-1200 cal. BP (Franco-Múgica *et al.* 2001; Rubiales *et al.*, 2012). In particular, the role of other important ecological factors such as anthropogenic fires and grazing/browsing has not been fully resolved. The paucity of well-dated multi-proxy palaeoecological records in the Northern Iberian Plateau may explain why these severe late Holocene forest fragmentation processes have not been investigated in depth yet.

Pinus nigra forests have a high ecological value as recognized, for instance, in the Annex I of the EU Habitats Directive and require specific conservation measures (Tíscar & Linares 2011). Increasing land abandonment in Mediterranean Europe during the last decades has favoured forest recovery (Weissteiner *et al.* 2011; Muñoz-Rojas *et al.* 2011) including *P. nigra* stands (Sheffer 2012). Under global change conditions, this afforestation trend may be counterbalanced by the occurrence of more frequent and intense wildfires (Ordóñez *et al.* 2005; Vázquez *et al.* 2015), given that *P. nigra* has no fire-resilient traits to cope with high-intensity, crown stand-replacing fires (e.g. lack of serotinous cones and resprouting ability; Tapias *et al.* 2004). However, very little is known about its long-term fire

ecology (Fulè *et al.* 2008; Leys *et al.* 2014) and the extent to which this species can deal with different climatic and disturbance regime conditions. Palaeoecology can fill this gap by providing baseline conditions under different climatic scenarios and guidance for management of threatened species (e.g. Willis & Birks 2006; Tinner *et al.* 2013).

In this paper we focus on a multi-proxy palaeoecological record (pollen, dung fungal spores, microscopic and macroscopic charcoal) from a well-dated high-resolution sedimentary sequence (Tubilla del Lago, called Tubilla onwards; Fig. 1) in an area where *P. nigra* is currently absent. Our goals are: (1) to reconstruct the vegetation history around Tubilla for the last 7500 years, before and after the *P. nigra* forest demise (1300-1200 cal. BP), (2) to assess how *P. nigra* responded to climatic and disturbance regime variability, in particular by providing quantitative, long-term fire activity reconstructions, and (3) to discuss how palaeodata can be relevant for future management of threatened species with high conservation value, such as *P. nigra*.

Material and Methods

STUDY SITES

Tubilla (41°48'30.30"N, 003°34'21.63"W, 900 m a.s.l.) is a small mire (approximately 5 ha) located on a valley bottom (Fig. 1). The climate is continental Mediterranean, with mean annual temperature of 11.5°C ($T_{January}$ = 3.4°C, T_{July} = 20.2°C), mean annual precipitation of 500 mm and pronounced summer drought ($P_{July\text{-}Septenber}$ = 71.6 mm). The mire was partially excavated in 2007 to create an artificial lake. Close to the mire, vegetation is composed of meadows (Poaceae, Cyperaceae) and reedbeds (*Phragmites australis* (L.) Cav.). The surrounding landscape is hilly and mostly composed of Miocene calcareous sediments. Apart from a narrow strip of garrigue shrubland with scattered *J. thurifera* bordering the mire, cereal fields dominate the landscape with some remnants of natural

woodland (*Q. ilex*, *Q. faginea*, *J. thurifera* and *Pinus pinaster* Ait.) and small pine afforestations (*Pinus sylvestris* L., *P. nigra*) on previously cultivated land. The second site, Espinosa de Cerrato (41°57'24"N, 003°56'06"W, 885 m a.s.l.), called Espinosa onwards, is a small mire (8.8 ha) located 35 km from Tubilla with comparable climate, bedrock and vegetation (Franco-Múgica *et al.* 2001). Large fires in the region are quite rare at present, because of fire suppression by farming practices (MAGRAMA 2002, 2012). The nearest *P. nigra* standing population is located at the foothills of the Iberian Range, *c.* 25 and 60 km from Tubilla and Espinosa, respectively (Fig. 1). *P. sylvestris* and *P. pinaster* natural populations are also present in the region, growing at higher elevations (i.e. cooler and more humid conditions) and on sandy soils, respectively (Fig. 1).

CORING, SEDIMENTARY SEQUENCE AND CHRONOLOGY

We retrieved a 745-cm long core in October 2009 from the deepest and undisturbed part of the Tubilla mire using a Russian corer. After coring, core sections were wrapped and kept at 4°C until sub-sampling. Sediment was mostly peat, interbedded with more silty and sandy layers (Fig. 2). The chronology is based on 12 AMS radiocarbon dates, mostly from terrestrial plant macrofossils (Table 1). As no indication of the presence of sedimentary hiatuses has been found, we assign the year of the coring to the top of the core. We rejected only one radiocarbon date as too young because the sample contained *Phragmites* roots (Table 1). We converted radiocarbon ages into calendar years using the program CALIB 7.1 (IntCal13; Reimer *et al.* 2013). We then modelled the age-depth relationship with a smoothing spline (smoothing parameter = 0.25) using CLAM (Blaauw 2010; Fig. 2), and checked the robustness of our model by applying different smoothing parameters. For the Espinosa sequence, seven ^{14}C dates were available from previous studies (Franco-Múgica *et al.* 2001; see Table S1 in Supporting Information). We improved the original age-depth

model, based on uncalibrated radiocarbon dates (Franco-Múgica *et al.* 2001), by fitting a smoothing spline (smoothing parameter = 0.2) using CLAM (Blaauw 2010; Fig. S1).

POLLEN AND COPROPHILOUS FUNGI

Eighty-eight sediment samples of 1 cm^3 from the Tubilla sequence were sampled every *c.* 8 cm, and treated following standard laboratory methods for pollen analysis (Faegri & Iversen 1989). *Lycopodium* tablets were added to estimate pollen and spore concentration (Stockmarr 1971). We used identification keys (Punt *et al.* 1976-2009; Beug 2004), photographic atlases (Reille 1992) and reference collections (*Universidad Autónoma de Madrid*, *University of Bern*) to identify the pollen types. Since diploxylon *Pinus* pollen cannot be differentiated at species level unambiguously, we supported our data with available macrofossil information for *P. nigra* from the same site and surrounding area (summarized in García-Amorena *et al.* 2011). Additionally, local pine presence around the site was assessed by identifying *Pinus* stomata in the pollen slides (Ammann *et al.* 2014) according to Trautmann (1953). *Quercus robur*-type was named *Quercus faginea*-type because this is the most frequent deciduous oak in the study area. We identified Cerealia-type pollen according to size (threshold 40 µm), pore diameter and annulus thickness (Beug 2004). The main pollen sum, which excludes pollen from aquatic/wetland plants and spores, was mostly greater than 300 pollen grains except for few levels with bad preservation. Finally, we used coprophilous fungal spores as a proxy for past local grazing activities (e.g. Gill *et al.* 2013; identified following van Geel *et al.* 2003) to check vegetation responses to grazing pressure.

Tubilla local pollen assemblage zones (LPAZs) were delimited using optimal partitioning by sums-of-squares (Birks & Gordon 1985); statistically significant zones were assessed by comparison with a broken stick model (PSIMPOLL; Bennett 1996). Finally, we used ordination techniques (Birks & Gordon 1985; ter Braak & Prentice 1988) to extract the

underlying gradients in the two pollen data sets with CANOCO 4.5. First, we used detrended correspondence analysis (DCA; Birks & Gordon 1985), with square-root transformation, detrending by segments and no down-weighting of rare species, to assess whether a unimodal or a linear model of species response fits our pollen percentage data. Given the rather short length of the DCA first axis gradient for both sequences (1.985 SD for Tubilla and 1.523 SD for Espinosa), we used principal components analysis (PCA; Lepš & Šmilauer 2003).

MICROSCOPIC AND MACROSCOPIC CHARCOAL

We took 1 cm^3 sediment samples every centimetre for macroscopic charcoal analysis, to assess local fire occurrence close to Tubilla (few kilometres around the site; Whitlock & Larsen 2001; Higuera *et al.* 2007). Samples (a total of 745) were soaked in a 10% sodium hexametaphosphate solution for 24 h to deflocculate the sediment and later in a 9% oxygen peroxide solution for another 24 h to bleach the non-charcoal organic matter. Samples were then sieved through a 100-µm mesh and charcoal particles were counted with a stereomicroscope at a magnification of 40×. Macroscopic charcoal concentrations (# cm^{-3}) were converted to charcoal accumulation rates (CHAR; # cm^{-2} $year^{-1}$) using sediment deposition rates (cm $year^{-1}$). We then interpolated CHAR values to the median sample resolution (10 years) to achieve a constant time interval. Finally, we used a three-step decomposition of CHAR (Long *et al.* 1998; Higuera *et al.* 2010) to identify peaks associated to local fire episodes. To model the low-frequency component of the CHAR series (background CHAR), related to regional fire activity, changes in fuel load availability and/or to taphonomic processes such as reworking and redeposition (Long *et al.* 1998; Whitlock & Larsen 2001), we fitted a locally weighted regression (lowess) with a 1000-year smoothing window.

The CHAR peak series (residuals) was then obtained by subtracting the background CHAR component from the raw CHAR curve. Finally, the third step involved the use of a threshold to separate the noise component (due to random variability, sediment mixing, distant fires or redeposition; Whitlock & Larsen 2001) from the peaks. We applied both a globally-defined and a locally-defined threshold approaches to account for the variability in charcoal production and deposition which could relate to changes in vegetation composition and/or fuel loads (Higuera *et al.* 2009). Then, we used a threshold above the 99.9th percentile of the noise distribution of the local CHAR peak series, modelled with a Gaussian mixture model (Gavin *et al.* 2006). A minimum count screening was performed to identify statistically significant peaks (Gavin *et al.* 2006). Inferred fire frequencies (IFF) and fire return intervals (FRI) from the identified fire-related peaks were then smoothed with a 1000-year window. To assess whether the local fire signal is well-separated from the noise component we also calculated a signal-to-noise index (SNI; Higuera *et al.* 2009; Kelly *et al.* 2011). Statistical analyses were performed using the program CharAnalysis (Higuera *et al.* 2009). Finally, we separated two groups of charcoal peaks according to their size following Colombaroli & Gavin 2010, and using the 99th percentile of a Gaussian mixture model (Charster 0.8.3, Gavin *et al.* 2006).

To assess regional biomass burning (0-100 km around the site; MacDonald *et al.* 1991; Whitlock & Larsen 2001; Conedera *et al.* 2009) we quantified microscopic charcoal on pollen slides (10-250 µm; Tinner & Hu 2003; Finsinger & Tinner 2005) on both sequences (Tubilla and Espinosa). This allowed comparing fire activity at different spatial scales ("local" from macroscopic charcoal and "regional" from microscopic charcoal), and their effects on vegetation dynamics (Tinner *et al.* 2006; Colombaroli *et al.* 2008; Vannière *et al.* 2008). Results are reported as CHAR (# cm^{-2} year^{-1}) which account for the changes in sediment deposition rate (year cm^{-1}), as inferred from the age-depth models.

Results

TUBILLA PALYNOLOGICAL RECORD

The small size of the two mires and their catchments (5-10 ha) make the relevant pollen source area mostly local to extra-local, i.e. representing vegetation growing in several hundred metres to a few kilometres from the mire (Sugita 1994; Conedera *et al.* 2006). The pollen diagram (Fig. 3) shows two statistically significant pollen zones separating a period dominated by *Pinus* (TUB-1, 7500-1200 cal. BP) from the following TUB-2 (1200 cal. BP-present) dominated by herbaceous pollen types (mainly Poaceae).

Zone TUB-1 shows high values of tree pollen (usually over 80%), with fluctuating values of *Pinus*, *Q. faginea*-type, *Q. ilex*-type and *Juniperus*-type. We then further divided TUB-1 into three subzones accounting for the relative changes of those taxa.

Pinus is the main pollen type in subzone TUB-1a (7500-2600 cal. BP) with values often exceeding 70% and associated with *Pinus* stomata (Fig. 3). Several *Pinus* macrofossils are also present in this period and one well-preserved full bud (440-446 cm deep, *c.* 4200 cal. BP) was identified as *P. nigra*. Several transient drops in *Pinus* percentages are coupled with increases in *Q. faginea*-type, *Q. ilex*-type and Poaceae. Dung fungal spore curves are discontinuous and with low values.

Subzone TUB-1b (2600-1800 cal. BP) shows lower *Pinus* pollen values (*c.* 60%) than before, and higher *Q. faginea*-type (10-20%), *Q. ilex*-type (*c.* 10%), and (to a minor extent) *Erica*, Poaceae and *Artemisia* over eight centuries. Previous decreases of *Pinus* (e.g. *c.* 5500, 4500 and 4000 cal. BP) were significantly shorter. No *Pinus* stomata or coprophilous fungi are instead found in this zone (Fig. 3), while first Cerealia-type pollen occurs at 2300 cal. BP.

In subzone TUB-1c (1800-1200 cal. BP) *Pinus* values again increase (70-90%) at the expense of *Q. faginea*-type and *Q. ilex*-type, and *Pinus* stomata are present. At the end of TUB-1c both Cerealia-type and dung fungal spore curves (e.g. *Sporormiella*-type) become almost continuous.

The transition between zones TUB-1 and TUB-2 (1400-1200 cal. BP) features the most marked change in the pollen assemblage, with *Pinus* sharply decreasing from 90 to 20% in less than a century (Fig. 3). Pine stomata almost disappear at the same time (*c.* 1300 cal. BP). Then, from 1200 cal. BP until present *Pinus* exhibits relatively low percentage values, with *Q. faginea*-type and *Q. ilex*-type varying between 20 and less than 10%, and shrub (*Erica*, *Calluna*, Lamiaceae, *Helianthemum*) and herb taxa (e.g. *Artemisia*, *Plantago*, Poaceae, *Rumex*) mostly increasing. The Cerealia-type curve is continuous (1-9%) and spores of coprophilous fungi are often recorded (especially *Sporormiella*-type, see Fig. 3).

TUBILLA AND ESPINOSA CHARCOAL RECORDS

Macroscopic CHAR estimated in the Tubilla sequence over the last 7500 years show rather fluctuating values (Fig. 4a), ranging from 10-30 # cm^{-2} $year^{-1}$ to over 60 # cm^{-2} $year^{-1}$ around 4500 and 1200 cal. BP. The reconstructions based on the globally- and locally-defined thresholds (Figs 4b-c) allow assessing whether fire episodes near Tubilla had consequences over forest structure and composition through periods of land use changes (Fig. 4d). The approach based on the globally-defined threshold detected a total of 23 statistically significant charcoal peaks (Fig. 4c), with a corresponding mean FRI of *c.* 300 years (95% confidence interval: 150-500 years) and generally corresponds with the highest CHAR peaks (Figs 4c-e). In contrast, the reconstruction based on locally-defined thresholds (Fig. 4b) also accounts for smaller peaks which occurred within each pollen zone. Since we are interested in the full range of fire variability that nowadays characterize *Pinus* stands (i.e.

surface fire regime; Fulé *et al.* 2008), we mainly focus on this reconstruction (Fig. 4e). This method identified a total of 38 statistically significant charcoal peaks (Fig. 4b), corresponding to a mean FRI of *c.* 200 years (95% C.I.: 150-250 years). Also, 6 of the 38 peaks (clustered at 5600-4300 and 1300-1200 cal. BP; Fig. 4d), distinguished by the Gaussian mixture model (Colombaroli & Gavin 2010), correspond to large peaks (CHAR over 60 # cm^{-2} $year^{-1}$; Figs 4a-b, S2), that are also highlighted by the globally-defined threshold approach (Fig. 4c). Moreover, these large peaks are coupled with the most relevant decreases in *Pinus* pollen percentages of the entire sequence (e.g. 1300-1200 cal. BP; Figs 3, 4d). The resulting IFF ranges between 2 and 9 fire episodes every 1000 years (Fig. 4e), with maxima around 7500 cal. BP, 2800 cal. BP and towards present (7 fire episodes/1000 years). The high SNI suggests that peaks are well isolated from the noise (background) component.

The estimated changes in biomass burning at a more regional scale (microscopic CHAR) from both the Tubilla and Espinosa sequences (Fig. 5), again show high fire variability over the last 7500 years, with maxima around 4500 cal. BP (Tubilla) and 1500 cal. BP (Espinosa). Also, in accordance to the macroscopic charcoal record (Tubilla), microscopic CHAR is particularly high during the demise of *Pinus* pollen (1300-1200 cal. BP), then decreasing towards the present (Fig. 5).

ORDINATION

PCA for both pollen sequences show rather similar underlying gradients (Fig. 6). For Tubilla, the first and the second axes of the PCA explain 54.2% and 8.6% of the total pollen data variance. In Espinosa, the proportion of variance in the pollen dataset explained is similar, with 44.7% explained by the first and 10.0% by the second axis. Overall, the first axis in each sequence reflects a gradient from dense pine forests towards more open communities (including Mediterranean *Quercus* woodlands, shrublands, grasslands and

cultivated fields), indicating that the transition from pine forests to more open ecosystems at 1300-1200 cal. BP is the most marked vegetation change (Figs 5-6) occurring at both sites. The second axis shows a gradient with Mediterranean mixed deciduous-sclerophyllous *Quercus* woodlands (*Q. faginea*, *Q. ilex*, *Rhamnus*), shrublands (*Erica*, *Cistus*, *Genista*), grasslands (Poaceae, *Rumex*, *Plantago*, *Artemisia*) and crop fields (Cerealia).

Discussion

LONG-TERM INTERACTIONS BETWEEN *PINUS NIGRA*, CLIMATE AND DISTURBANCE REGIMES NEAR TUBILLA BETWEEN *C.* 7500 AND 1400 CAL. BP

The reconstructed vegetation changes at our mid-elevation site (Tubilla) show a long lasting, *c.* 6000 years (7500-1400 cal. BP), dominance of pine forests, in agreement with other palaeoecological records from the eastern part of the Northern Iberian Plateau (Fig. 1). The finding of several *P. nigra* macrofossils in our same record (buds, cones; Table 1; García-Amorena *et al.* 2011) together with the continuous record of pine stomata (until 1300 cal. BP; Fig. 3) suggest the local dominance of *P. nigra* in our study area until at least 1400 cal. BP, in contrast to its present-day fragmented populations (Fig. 1). Other pine species such as *P. sylvestris* and *P. pinaster* were also probably present in the region, but possibly restricted to more humid areas at higher elevations and to sandy soils, respectively (Costa *et al.* 2005). We compare long-term vegetation and fire dynamics around Tubilla to available palaeoclimatic evidence in the area to understand the extent to which *P. nigra* forests were able to withstand past climatic and fire variability before their final collapse at *c.* 1400-1200 cal. BP.

Palaeoclimatic data suggest that Mediterranean Iberia experienced a trend towards drier conditions during the last 5000-6000 years (Carrión 2002; Morellón *et al.* 2009; Aranbarri *et al.* 2014, 2015), with the driest episodes at 5800-5400, 4300-3800, 3100-2600,

2200-1700, 700-500 and 300 cal. BP (Carrión 2002; Fig. 4g). Notwithstanding these marked multi-centennial fluctuations in the moisture balance, our data suggest that only relatively minor retreats in pine forests occurred around Tubilla (Fig. 4) and also in the region (Fig. 5; Franco-Múgica *et al.* 2005; García-Antón *et al.* 2011). For instance, around Tubilla major dry events around 5500, 4000 and 3000 cal. BP (Fig. 4g) caused only temporary retreats of *Pinus nigra* forest (from 80-90 to 60%; Fig. 4d), while other brief declines such as that around 4500 cal. BP seem unrelated to moisture availability. Thus, the observed range of Holocene climatic variability in Mediterranean Iberia did not result in any significant, long-lasting *P. nigra* forest reduction, suggesting that this species is resilient to natural drought variability and able to cope with a broad range of climatic conditions (Costa *et al.* 2005). Rather, its dominance over millennia in the eastern part of the Northern Iberian Plateau was probably supported by strong climatic seasonality and shallow calcareous soils, favouring this species over the more drought-sensitive *Quercus faginea* (Franco-Múgica *et al.* 2001; Granda *et al.* 2013; Forner *et al.* 2014). In contrast, Holocene drought episodes were probably not so pronounced to cause the replacement of *P. nigra* with more drought-tolerant species such as *Juniperus thurifera* and *Quercus ilex* (Costa *et al.* 2005; Granda *et al.* 2013).

Pinus nigra was also able to cope with the centennial to millennial fire variability observed in our records (Figs 4, 5). For instance, our reconstructed fire history shows how wildfires were relatively common during the phase when *P. nigra* dominated (Figs 4d-e), highlighting the importance of fire for pine forest dynamics. More specifically, our fire reconstructions show that *P. nigra* forests were able to cope with variable fire frequencies ranging from 2 to a maximum of 9 fires/1000 years (corresponding to FRI of 110-500 years). This is in agreement with other long-term records in the Mediterranean showing that *P. nigra* can withstand IFF up to 12.5 fires/1000 years (corresponding to a FRI of 80 years; Leys *et al.* 2014). Many ecological data show that *P. nigra* is able to survive surface burning (Fulé *et al.* 2008; Christopoulou *et al.* 2013), due to fire resistant traits such as self-pruning and thick

bark (Tapias *et al.* 2004). Surface fires have also been shown to indirectly promote seedling establishment in the shade-tolerant *P. nigra*, by reducing ground-level competition (Ordóñez *et al.* 2004; Lucas-Borja *et al.* 2011; Valor *et al.* 2013). In contrast, *P. nigra* is highly sensitive to crown fires, with slow post-fire recovery due to the lack of serotinous cones and seed sensitivity to heat (Escudero *et al.* 1999; Tapias *et al.* 2004). In our record, significant but short-lived changes in both composition and structure of pine stands occurred when fire activity exceeded the long-term norm (CHAR over a threshold of 60 # cm^{-2} $year^{-1}$; around 5500, 4600 and 4200 cal. BP, see red triangles in Fig. 4d). We assume that such high amplitude events correspond to a fire regime characterized by intense/severe events, probably crown fires, as also suggested by the two significantly separated populations of charcoal in the Gaussian mixture model (Colombaroli & Gavin 2010). Interestingly, these fire episodes occurred during periods of increased dryness in Mediterranean Iberia (Carrión 2002; Fletcher *et al.* 2013; Fig.4g). Such events were of sufficient magnitude to cause marked retreats of pine forest (from 80-90 to 60%; Figs. 3, 4d), with temporary replacements with more fire-adapted communities, such as *Q. faginea/Q. ilex* woodlands (resprouters) and grasslands. Transient replacement of *P. nigra* with grasslands, shrublands, deciduous and sclerophyllous *Quercus* woodlands (Fig. 3) has also been reported from NE Iberia following severe fires (Retana *et al.* 2002; Rodrigo *et al.* 2004). Taken together, secondary successions following fire disturbances ended with full *P. nigra* forest recovery (Fig. 4d), showing that *P. nigra* ecosystems were able to cope with a wide range of climate and fire variability, highlighting the important role of *P. nigra* in Iberian ecosystems (Carrión 2002; Rubiales *et al.* 2010; García-Amorena *et al.* 2011).

CAUSES OF THE REGIONAL-SCALE DEMISE OF *PINUS NIGRA* FORESTS AROUND 1400-1200 CAL. BP

Around Tubilla, the dominance of *P. nigra* forests persisted until 1200 cal. BP, when *Pinus* underwent a relatively fast collapse (from *c.* 90 to 20% in less than a century, Fig. 4d) unprecedented in the context of the last 7500 years (Figs 3, 6). Given that the species did not recover, this period around 1200 cal. BP left a distinctive legacy on the currently fragmented distribution of *P. nigra* forests (Fig. 1b). Our data show that this demise started with three almost consecutive episodes of high fire activity (CHAR > 60 # cm^{-2} $year^{-1}$) occurring between 1300 and 1200 cal. BP (see Fig. 4d). Three large macroscopic CHAR peaks (between 1300 and 1200 cal. BP) may correspond to stand-replacing crown fires, which triggered *P. nigra* demise, given that this pine species is not adapted to regenerate after complete combustion (e.g. Tapias *et al.* 2004; Rodrigo *et al.* 2004). This period of high fire activity was followed by the expansion of crops (Cerealia reaches 9%, Fig. 4d) and pastures (obligate coprophilous fungi up to 5%, Fig. 4d) in the area. Therefore, our data strongly suggest human impact through forest clearance and slash-and-burn as the main driver of pine forest collapse (see also Franco-Múgica *et al.* 2001).

The archaeological record shows that human settlements close to Tubilla were already present during the Iron Age (2600-2500 cal. BP; Martín-Valls 1986; Fig. 4f), thus several centuries before the observed collapse of *P. nigra* in our record. In agreement, a first Cerealia-type signal associated with a marked increase in *Plantago* at Tubilla suggests minor arable agricultural activities at *c.* 2500 cal. BP. Local human settlers took advantage of the forest for localized logging (Rubiales *et al.* 2011; Aranbarri *et al.* 2015), with less importance of agricultural and grazing practices (Cerealia and dung fungal spores only increased at 1300-1200 cal. BP; Fig. 4d). Under such localized disturbances, *P. nigra* stands were apparently able to recover within few centuries at most (*Pinus* pollen *c.* 60%; Fig. 4d), being replaced in the meantime by disturbance-adapted resprouters such as oaks. This

pattern differs from other Mediterranean areas where marked changes in both vegetation composition and structure occurred already during the Neolithic (e.g. Colombaroli *et al.* 2008, 2009; Tinner *et al.* 2009; Carrión *et al.* 2010).

Medieval pine forest clearance was a widespread process in the Northern Iberian Plateau following land-use intensification, and the final pine demise and establishment of cereal fields occurred almost synchronously in the eastern part of the Northern Iberian Plateau (Fig. 5; Franco-Múgica *et al.* 2001; Aranbarri *et al.* 2015). At our sites, the conversion of pine forests to more open habitats occurred at *c.* 1200 cal. BP, mainly induced by agriculture and grazing intensification. This land-use largely prevented pine forest regeneration through deliberate fires (Figs 4-5). When the town of Tubilla was founded *c.* 1100 cal. BP (Fig. 4f; Cerezo *et al.* 2009) the Northern Iberian Plateau was the border between the Christian and Muslim kingdoms and fire was often employed for war purposes (Corella *et al.* 2013). This use of fire documented during the Arab incursions into this area during the VIII-IX centuries AD (1250-1050 cal. BP; Martínez-Díez 2005) probably accelerated the demise of pine forests. At this time and later, local and partial pine recoveries occurred (e.g. at 1100 and 700 cal. BP at Espinosa; Fig. 5), but they were only short-lived and never allowed pine forests to attain pre-medieval conditions.

Together, our palaeoecological data suggest that present fragmented landscapes originated mainly during medieval times when the region was the frontier between Christian and Muslim kingdoms. Fire was the main driver for the rapid landscape conversion to secondary succession communities (Figs 3-5), probably facilitated by drier conditions at that time (Fig. 4g; Domínguez-Castro *et al.* 2014). This use of fire to open the landscape caused post-fire regeneration failure in *P. nigra*, which was replaced by oak woodlands (*Q. faginea*, *Q. ilex*) or cereal fields within few decades (Figs 3, 4d). The strong resprouting ability of oaks (*Q. faginea*, *Q. ilex*) explains their primary role in determining post-fire succession in this area at both decadal (Retana *et al.* 2002; Rodrigo *et al.* 2004) and longer timescales (Fig. 3).

CONSERVATION OF *PINUS NIGRA* POPULATIONS UNDER CURRENT AND FUTURE CHANGES

At present, *Pinus nigra* subspecies *salzmannii* (Dunal) Franco is almost extinct in the Northern Iberian Plateau, in contrast to other areas with similar climatic conditions where it is still relatively widespread (mountains of eastern Iberia; Costa *et al.* 2005). Palaeobotanical data (Fig. 1b and references therein) show that this species was indeed a primary element of Iberian forests before medieval times and fully supports its native status in the region, under a wide range of climate (Fig. 4g) and disturbance regimes (Figs 4, 5). In accordance to other palaeoecological evidence (Leys *et al.* 2014), our high-resolution data suggest that *P. nigra* is adapted to fire prone environments, showing resistance to moderate ground fires (Fig. 4d). The species can also recover after rather severe disturbances within one or two centuries. On the other hand, our data show how *P. nigra* ecosystems were poorly resilient (both resistance and recovery rate, Hodgson *et al.* 2015) to excessive anthropogenic disturbance including slash-and-burn for arable and pastoral farming (Fig. 4).

The maintenance of relicts of *P. nigra* forest will highly depend on future land-use changes, which may cause further reduction in *P. nigra* stands, leading to irrecoverable losses (Puerta-Piñero *et al.* 2012; Martín-Alcón & Coll 2016). Future drier conditions and higher temperatures (e.g. IPCC 2013; Sousa *et al.* 2015) may also increase the occurrence of high-severity fires and threaten even more these relict stands. Thus, counter-measures to restore the natural disturbance variability observed in the long-term (Fig. 4), by reducing fuel load accumulation and/or prescribed burning (e.g. Stephens & Moghaddas 2005; Santana *et al.* 2011) might be effective conservation strategies. Conversely, further land abandonment scenarios in the region (Weissteiner *et al.* 2011; Muñoz-Rojas *et al.* 2011) may favour *P. nigra* re-expansion within few decades, causing changes in fire variability (Figs 3-5).

Long-term data provide valuable insights into the potential of Mediterranean species that underwent range contractions due to land-use intensification (Colombaroli *et al.* 2007;

Rubiales *et al.* 2012; Morales-Molino *et al.* 2013; Tinner *et al.* 2013). Our data thus suggest that *P. nigra* should be indeed considered a primary target species for reforestation efforts in this area, in light of its economic (timber production) and ecological (soil protection, biodiversity) values. Surprisingly, this species has been only marginally considered for recent reforestation efforts in the region (JCyL 2014). In this sense, long-term data can provide a reality check for assessing future responses of *P. nigra* or other native Mediterranean species to ongoing changes.

Authors' contributions

C.M.M., W.T. and D.C. conceived the ideas and designed research; C.M.M. and M.G.A. acquired the data; C.M.M. and D.C. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The data used in this study has been included in the Supporting Information. Charcoal data will also be available through the Global Charcoal Database (www.paleofire.org) and pollen data, through the European Pollen Database (www.europeanpollendatabase.net) after publication.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table 1. Radiocarbon dates for Tubilla del Lago. All calibrated dates were obtained using CALIB 7.1 (Reimer *et al.* 2013).

Laboratory code	Depth (cm)	Material	^{14}C age (^{14}C BP)	Calibrated age (cal. BP, 95.4% confidence interval)	Calibrated age (cal. BP, median)
BE-3042	88-90	*Carex* seeds and fruits, charred plant material	1150 ± 40	973-1176	1064
Beta-245872	99-100	(Silty) peat	1230 ± 40	1063-1267	1163
BE-3041	144-150	*Carex* seed, charcoal, periderm	1480 ± 30	1306-1411	1364
UBA-25013	198.5-199	Silty peat	1490 ± 25	Rejected	Rejected
BE-3040	222-226	*Pinus* bud, charcoal	2380 ± 55	2321-2701	2436
UBA-25014	333-333.5	Peat	2960 ± 30	3005-3211	3121
UBA-25015	401.5-402	Peat	3490 ± 30	3649-3842	3765
BE-3039	440-446	*Pinus nigra* bud, *Pinus* needles	3830 ± 25	4103-4401	4223
Beta-245873	499-500	Peat	3950 ± 40	4256-4520	4411

UBA-25016	629.5-630	Peat	5330 ± 30	5999-6203	6106
BE-3038	636-644	Conifer bud scales, *Carex* seeds, charcoal	5520 ± 50	6213-6408	6323
Beta-245874	734-735	(Silty) peat	6520 ± 40	7325-7507	7438

FIGURE CAPTIONS

Figure 1. (a) Location of the Northern Iberian Plateau in north-western inland Iberia. Our study area lies on the western edge of the current distribution range of *Pinus nigra* (modified from EUFORGEN, 2009; www.euforgen.org). Out of the six different subspecies of *P. nigra* (Barbéro *et al.* 1998), subspecies *salzmannii* is the only native one from the Iberian Peninsula **(b)** Location in the Northern Iberian Plateau of Tubilla del Lago, Espinosa de Cerrato and other palaeoecological sites mentioned in the text, as well as the current distribution of the main pine species growing in the study area, i.e. *P. nigra*, *P. sylvestris* and *P. pinaster*. Pollen sites: 1 Tubilla del Lago (this paper); 2 Espinosa de Cerrato (Franco Múgica *et al.* 2001; this paper); 3 Conquezuela (Aranbarri *et al.* 2015); 4 El Carrizal (Franco-Múgica *et al.* 2005); 5 Camporredondo (García-Antón *et al.* 2011). Sites with *P. nigra* macrofossils: 6 Tubilla del Lago, 7 Cevico Navero, 8 Lomilla, 9 Tubilla del Agua, 10 Fuentetoba (all summarized in García-Amorena *et al.* 2011); 11 Villatoro (Rubiales & Génova 2015).

Figure 2. Age-depth model for Tubilla del Lago (black, continuous line); the grey envelope represents the 95% confidence intervals of the estimated ages. The lithostratigraphy column (left) shows sediment changes from peat to silty peat, and the

relative position of the main sandy layers following intensified erosion in the catchment around 4100, 3000, 2600-2500 and 1200 cal. BP.

Figure 3. Pollen percentage diagram from Tubilla del Lago (selected types). Empty curves represent 10× exaggeration. **(a)** Trees, shrubs and microscopic charcoal. **(b)** Herbs, microscopic charcoal, aquatic plants, ferns and dung-related fungal spores. In total, we identified 113 pollen and fern spore types.

Figure 4. Tubilla del Lago: quantitative fire reconstruction and interaction with long-term vegetation, land use and climate variability. Grey bars correspond with the main archaeological/historical periods at the study area. **(a)** Macroscopic CHAR (charcoal accumulation rate) series interpolated to the median sample resolution, i.e. 10 years. BCHAR curve represents the background component of the macroscopic CHAR series, with maxima at *c.* 7500, 4500 and 1200 cal. BP. **(b)** Local fire episodes identified with locally-defined thresholds. Red dots represent "big" peaks (i.e. above the 99th percentile of a Gaussian mixture model), and are mostly associated with sharp decreases in *Pinus* pollen percentages (red triangles in d). Blue dots are instead "small" peaks. **(c)** A more conservative fire reconstruction using a globally-defined threshold and highlighting the frequency of the largest peaks (see text). **(d)** Selected pollen and spore curves illustrating major vegetation changes (*Pinus*) and human land-use (Cerealia, obligate coprophilous fungal spores). Note the different scales of the two vertical axes. **(e)** Positive residuals of the CHAR series and local inferred fire frequency (IFF) using locally-defined thresholds. **(f)** Documented historical events or archaeological findings: (1) Iron Age settlement at Pinilla Trasmonte (6.5 km distant from the study site) dated at 2600-2500 cal. BP (Martín-Valls 1986), (2) Roman settlements in Baños de Valdearados and Valdeande (both are about 5

km apart from Tubilla; Argente 1979; Figuerola 1988) dated at 2000-1600 cal. BP, and (3) Christian-Muslim wars north of the River Duero and foundation of the town of Tubilla del Lago at *c.* 1000 cal. BP (Cerezo *et al.* 2009). **(g)** Decadal-to-centennial dry phases in Mediterranean Iberia: (g.1) historical archives Al-Andalus (Domínguez-Castro *et al.* 2014) and (g.2) Lake Siles (1320 m a.s.l.; Carrión 2002). Note that within the chronological uncertainties, the first three "big" peaks (at *c.* 5600, 4700 and 4300 cal. BP) are associated with dry phases.

Figure 5. (a) *Pinus* and Cerealia-t. pollen percentages at Tubilla del Lago (a.1; this study) and Espinosa de Cerrato (a.2; Franco Múgica *et al.* 2001). **(b)** PCA axis 1 for Tubilla del Lago (b.1) and Espinosa de Cerrato (b.2) pollen sequences. **(c)** Microscopic CHAR for Tubilla del Lago (c.1) and Espinosa de Cerrato (c.2). Shaded bars depict the time interval when major pine forest demise (*Pinus* pollen percentages drop from around 90% to 10-20%) occurred in the Northern Iberian Plateau.

Figure 6. PCA bi-plots of species vectors (arrows) and sample (symbols) scores. Different symbols represent the various local pollen zones/subzones. Colours show pollen zones before (until *c.* 1300-1200 cal. BP, red symbols) and after (blue symbols) pine demise. Different symbols represent the different local pollen zones/subzones in Fig. 3.